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Unisex Flash Controls in Dialog Fireflies

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Abstract. During courtship in many dialog fireflies, the female flashes at a fixed interval after each rhythmic display signal of the male. The male then orients toward her flash, but does not flash in response. In three species, males also may decoy other males by answering them after an interval equal to the female's characteristic flash delay. In two other species, individuals have been induced to respond to, or to duplicate, interflash intervals characteristic of the opposite sex. Both male and female thus harbor overt or latent homologs of some of the other's flash-timing circuits.

Introduction

The lock-and-key nature of many courtship communication systems shows that one sex has a suite of behavioral controls that fit those of the other. Quantitative interdigitation of stimulus and response is perhaps nowhere shown more starkly than in the timed dialogs of certain fireflies. In *Photinus pyralis,* for example, the flying male emits spontaneous advertising flashes at about 6-s intervals, hovering for about 2 s after each flash. The sedentary female flashes only responsively, about 2 s after seeing a flash of the male. If the male sees a flash 2 s after his flash, he flies toward it. The characteristic 2-s response delay of the female is the necessary and sufficient signal for the orientation of the male (Buck, 1937). Therefore, the nervous system of the male undoubtedly contains an endogenously activated, 2-s window-opening circuit that is tuned to the visually activated 2-s flash-control circuit of the female.

In typical time-coded courtship dialogs, the female is the responder and the male the advertiser. The male ordinarily flashes rhythmically; the female responds after a relatively fixed delay. The female-male interflash interval therefore tends to have a regular duration. However, this does not mean that the male flashes in response to the female's answer to his preceding flash. Rather, the regularity of the female-male interval is an artifact of the male's ordinarily rhythmic flashing. If he has to detour around or over obstacles, his flash may be long-delayed. Females remain responsive for many minutes without photic input.

Though dialog males do not flash in response to the female's answering flash, they may give photic responses under other circumstances. During the courtship of *Luciola lusitanica,* the male flashes about once per second, and the male-female delay interval, the key to recognition of the female by the male, is about 0.3 s (Papi, 1969); but Papi also observed instances in which the flash of a flying male triggered a flash by a male in the grass, after a delay of about 0.3 s. Males giving such "homosexual" (sic) responses remained on foot and sometimes, by answering flying males repeatedly, induced them to land. This behavior is thus unusual both in involving male-male photic interaction and because the response simulates the normal delayed response of the conspecific female. Papi recognized that ". . . to some extent [the behavior] is identical in the two sexes, indicating unsuspected common central [nervous] mechanisms."

In *Photinus concisus,* the male's flashing period is about 2 s and the female's code-key response delay is about 0.6 s (Lloyd, 1968). In this species, perching males often attract flying males by responding after a delay of 0.6 s (Buck and Buck, unpub.). Similarly, grounded males of *Photinus aquilonius* sometimes answer a flashlight signal after about the female's normal delay interval (Dr. Sara Lewis, pers. commun.).

Though males of the above-mentioned three species sometimes flash a response to other males after a delay equal to the normal male-female response delay, no con-

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Abbreviations: LED = light-emitting diode; STR = straight-ahead flight; CIR = circular flight; SD = short delay; and LD = long delay.

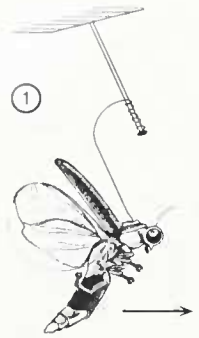

Figure 1. Lateral view of male attached to STR suspension of No. 30 chromel wire. Not to scale (actual length of insect, 15 mm; of insect-to-pin wire, about 30 mm).

sistent behavior of this sort has been described in either *Photinus pyralis* or *P. greeni* during many years of study. Flying male A of *P. pyralis* may indeed orient toward the flash of flying near-neighbor B, if B happens to flash about 2 s after one of A's flashes. However, A does not flash an answer to B, and B pays no attention to A, so the attraction breaks down.

Flying males of *P. pyralis* may also be stimulated to flash, but not orient, by the flash of another male flying nearby. This occurs during synchronized flashing (Buck, 1935) and between males flying and flashing indoors in total darkness (Buck, 1938a), but the delay involved is less than half a second. The quantitative relationships of this short-delay response to the 2-s orientational response, and to the normal 6-s flashing period, are virtually impossible to obtain from photometer measurements on a given male in the field, because of the unpredictable changes in direction, velocity, altitude, recording distance, and body orientation during flight. The relationships are also impossible to obtain from captive (perched) males because such animals rarely flash spontaneously, and never regularly.

In an effort to induce males to flash rhythmically from a fixed position that would permit controlled photic stimulation and recording, I attempted to induce flight in tethered specimens in the laboratory. As will be shown, this technique did permit recording of spontaneous flashing and of normal photic responses. Unexpectedly, it also evoked a new behavior suggesting that circuitry mediating response at the female's characteristic delay interval is present in the male in latent form.

Materials and Methods

The principal laboratory data were derived from *P. pyralis* males collected near Bethesda, Maryland, during June and early July of three seasons. Supplementary measurements were made on Baltimore males studied in Woods Hole, Massachusetts, during late July and early August of a fourth season. Field observations totalled ten years.

Netted specimens were stored in closed 10-ml plasma vials humidified with a chip of raw apple, and were used at various times over several days at 23° to 26°C. Two types of suspension, pivoting on No. 2 insect pins, were used in inducing tethered flight. On one (STR; Fig. 1) the male maintained a fixed direction. On the other (CIR; Fig. 2) the animal flew in a tight circle. The suspensions held the animals a few cm above a black benchtop.

Specimens were immobilized with carbon dioxide or on a chilled porcelain plate, and the suspension was cemented to the center of the pronotum with a droplet of low melting point dental wax, using an electrically heated needle (Buck, 1938b). After mounting, the specimen was given an 8 × 8 mm slip of filter paper, dampened with sucrose water, to hold and drink from. Rectangular flashes of 0.4 s duration, from a green light-emitting diode (LED; Monsanto MV5253), were the standard photic stimulus. These were delivered at a level slightly below the firefly, 15–20 cm from the pivot. For the STR males the stimuli were lateral. Flashes were detected at bench level with an RCA 1P21 photomultiplier photometer 25–30 cm from the pivot, and recorded on a chart recorder at 25 mm/s (Buck and Buck, 1968). Stimulus-response delays were measured on the chart from rise to rise, with a time resolution of 0.01 s.

In testing, the pivot pin was positioned in cork so as to hold the animal in correct flight attitude. Light intensity at the firefly's level was reduced to typical evening field level (5–20 lux) by replacing the room light with a single shielded 40-W S11 lamp reflected off a whitish sound-tile ceiling eight feet above the bench. (This level of illumination enables one to see head and abdominal movements.) The tarsal flight reflex was then evoked by removing the filter paper from the feet. Occasionally, flight initiation was encouraged by blowing on the insect.

Significance of differences between means was as-

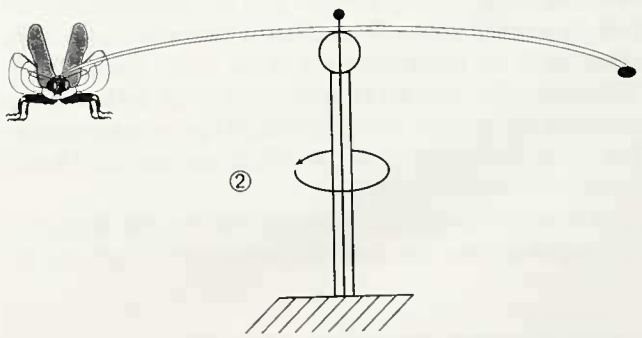

Figure 2. Facing male mounted on CIR suspension consisting of a 22 cm × 2 mm strip of thick photographic film resting on glass bead. Pronotal end of strip tapered. Other end with wax bead tare. Not to scale.

sessed by Student's *t*-test. Mean response delays are given with standard deviations (s), not standard errors. In making comparisons, variance is indicated by V, the coefficient of variation (s/M).

Results

Flight

On both suspensions, about two thirds of the hundred-odd males mounted flew reliably; about two thirds of those flying responded to LED stimulation. Flight variability was possibly due to the difficulty in mounting the animals so that the suspension did not touch the spread elytra or antennae; response variability was perhaps due to the body not being in exactly the normal flight attitude [head extended forward from under the nearly horizontal pronotum, thorax inclined downward toward the rear about 30°, abdomen hanging down almost vertically, directing the light from the ventral lanterns in the 6th and 7th segments downward and forward (Fig. 1)]. The flight reflex is very compelling; males will even fly upside-down.

With both suspensions, many continuous flights of up to 30 min were observed, and some animals flew on more than one day if demounted between flights. Wingbeat frequency of STR animals was found stroboscopically to be about 80 Hz at about 25°C. Flying STR animals sometimes writhed the abdomen, a behavior that *P. pyralis* does not exhibit in normal flight. STR males that flashed spontaneously (*i.e.*, more than 4 s after an LED flash; see Discussion) showed no flight change corresponding to the dip and hover behaviors that are normally associated with flashing during field display. When given an LED answer about 2 s after flashing, males sometimes turned the head immediately toward the signal (video observations with J. F. Case). Presumably this was the functional equivalent of the normal response in which the body turns as a whole.

Many CIR records showed an artifact due to ambient light reflected off or interrupted by the rotating arm (Figs. 7a, 16, arrows). From the typical, indicated 2-Hz rate of rotation, and the 11-cm radius of rotation, the velocity of linear flight was calculated to be about 3 mph. Rate of rotation was constant.

The results reported below suggest that a normally hidden 2-s flash-control circuit of the *P. pyralis* male was sometimes revealed by forcing the animal to fly in a circle. As a control background for this hypothesis, I therefore first present full ranges of both the spontaneous flashing and the short-delay photic responses of both STR and CIR males.

Spontaneous flashing

Flashing in the absence of stimulation was usually sporadic, but, on both suspensions, some males flashed spontaneously and consecutively for a number of cycles in approximately the normal rhythm. These spontaneous flashes were sometimes quite uniform in intensity and were emitted as regularly as by males flashing in the field. The STR series of Figure 3, for example, shows uniform flashes and regular rhythm. In contrast, the Figure 5 STR series illustrates flashes that were highly variable in form (perhaps because of abdominal twisting), though emitted with respectable regularity (see figure legends). With the CIR suspension, apparent flash intensity, contour, and duration varied widely as the animal rotated and the ventral abdominal lantern was alternately partly occluded and then exposed to the photometer, but rhythmic flashing was nonetheless observed (Fig. 7 and legend).

Short-delay photic response (SD)

The effects of exposing flying males to LED flashes were quite variable in mode, between individuals, and between suspensions, and often the firefly did not flash for many seconds after a signal. Two types of consistent response were observed. In the more frequent, seen in animals on both suspensions, the male flashed from 0.2 to 0.7 s after the LED stimulus. Many hundreds of these "triggerings" were recorded from the dozens of males studied. Figures 4 and 9–14 illustrate variations in flash form and delay observed in six STR males, and Figures 8 and 16–18 do the same for two CIR animals. Mean response delays for individual males ranged from 0.26 $\pm$ 0.02 s to 0.46 $\pm$ 0.08 s, and some differed significantly from each other. Mean delay ranges for individual males were typically less than 0.15 s.

CIR animals tended to respond after somewhat longer delays, and flash more dimly, than STR animals, although there were substantial overlaps. I found that males walking on a smooth horizontal surface did not respond to flashed answers to their signals if the answer was delivered from directly behind or from the rear within 30° to either side of the longitudinal body axis. This means that CIR males might have been unable to see the LED signals for up to 1/6 revolution (*ca.* 0.083 s).

When apparent CIR delays were each reduced by an average blind-spot correction (0.04 s), the overall mean delay duration was not significantly greater than that of STR animals at the same temperature. Ninety-five percent of both STR and CIR measurements fell between 0.25 and 0.65 s. For the present, accordingly, the most parsimonious conclusion is that STR and CIR males give the same short-delay photic response. The narrow frequency distribution peaking at 0.4 s in Figure 19 is the averaged delay for STR and CIR males. The mean delay for the combined group was 0.38 s.

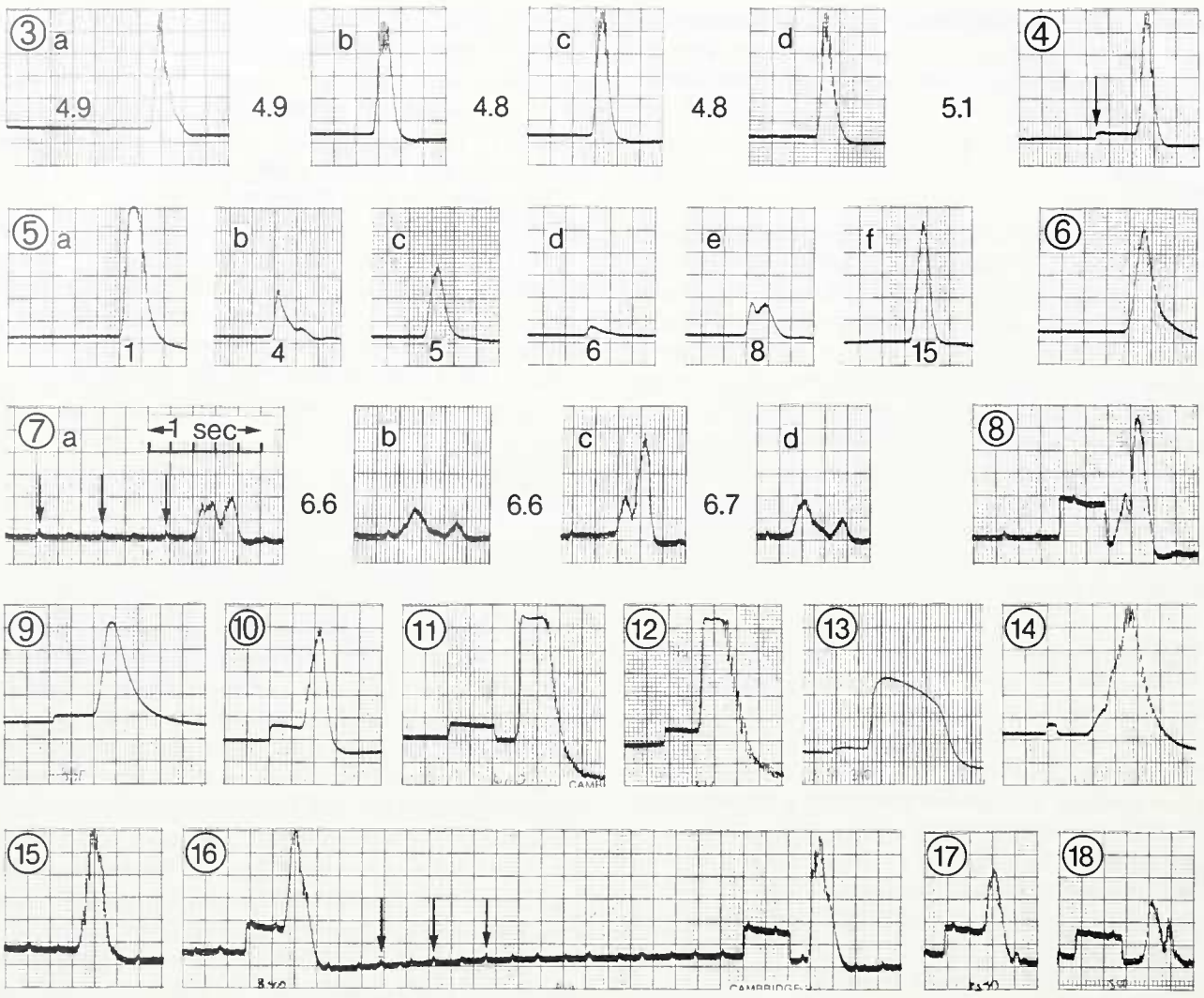

Figure 3. Four successive spontaneous flashes of STR male 126, a–d, flashes 2–5 in a rhythmic series of 8 (mean period 4.92 ± 0.16 s; V = 3). Numbers are flash-to-flash intervals. T = 25°. Note: in the chart records, the rapidly rising and falling limbs of some flashes have been reinforced. Jagged or sawtooth traces are instrumental AC noise revealed by high amplification. Decline of traces below baseline after some flashes is an instrumental artifact. Flash intensity is arbitrary. Time scale for all records indicated on Figure 7a. **Figure 4.** SD response of STR male 126 to 0.4 s LED stimulus. Delay 0.35 s, showing stimulation at the LED "on" phase (arrow). **Figure 5.** Rhythmic spontaneous flashing of STR male 124, a–f, flashes 1, 4, 5, 6, 8, and 15 in a series of 27, showing variability of flash intensity and form. Record also showed a 0.4-s difference in mean delay between two sections of same run: mean of first 13 cycles, 6.06 ± 0.41 s (V = 6); mean of last 14 cycles, 6.46 ± 1.04 s (V = 16). **Figure 6.** Spontaneous flash of STR male 132. T = 25°. **Figure 7.** Four consecutive spontaneous flashes of CIR male 94, a–d, flashes 9–12 in rhythmic series of 13, showing 0.55 s rotation artifacts (arrows in a) and effects of rotation on flash form delineation by photometer. Numbers, interflash intervals. Mean period for series, 7.2 ± 0.93 (V = 13). T = 22°. **Figure 8.** SD response of CIR male 94. Delay 0.46 s. **Figure 9.** SD response of STR male 1. Delay 0.36 s. **Figure 10.** SD response of STR male 98. Delay 0.28 s. **Figure 11.** First of two consecutive SD responses of STR male 105 that were 5 s apart. Peak clipped by over-amplification. Delay 0.60 s. **Figure 12.** Next SD response of STR male 105. Delay 0.3 s. **Figure 13.** SD response of STR male 282, showing 0.8 s flash duration. Delay 0.3 s. T = 27°. **Figure 14.** SD response of STR male 123 to 0.1 s LED flash, showing slow light accretion but typical 0.37 s delay. **Figure 15.** Spontaneous flash of CIR male 107. T = 23°. **Figure 16.** Two consecutive SD responses of CIR male 107, 4.4 s apart. First delay, 0.37 s; second delay, 0.58 s. Arrows, rotation artifact. **Figure 17.** SD response of CIR male 107 showing delay of 0.35 s, close to that of first flash in Figure 16, but of lower intensity. **Figure 18.** SD response of CIR male 107, showing delay of 0.56 s, close to that of second flash in Figure 16, but of lower intensity, and distorted by rotation of suspension.

Long-delay photic response (LD)

A second, less frequent type of photic response (Figs. 20, 22–24; filled columns in the 1.5 to 3 s range in Fig. 19) was given only by CIR males. In 15 of 31 individuals, from 1 to 23 such responses, with delays averaging 2.3 s, were recorded, sometimes several in succession. No flashes in the 2–3 s post-stimulus range were seen in any of 20 different males flying from the STR suspension. In some instances, the CIR firefly's response flash was followed by a second, spontaneous flash at about the same interval (Fig. 24). On several occasions, two spontaneous flashes about 2.3 s apart were emitted (Figs. 21, 24; unfilled column caps in Fig. 19).

In sum, LED stimuli evoked two photic responses: a short-delay (SD) variety—delayed an average of 0.38 s (Fig. 19, first distribution frequency peak); and a long-delay (LD) one—delayed an average of 2.3 s (Fig. 19, 1.5 to 3 s concentration). Both distributions were shown to be significant ($P > 95\%$) by Wallenstein's (1980) scan statistic, using an 0.5-s window. With one exception among hundreds of records (Fig. 23), LED stimulation evoked one response or the other, not both.

Discussion

Spontaneous flashing

In experiments on intact fireflies, there is no direct way of ascertaining which flashes are initiated endogenously and which are responsive. In the present work, absence of significant clumping of flashes later than 3 s after LED stimulation (Fig. 19) indicates that the SD and LD distribution peaks reflect true photic responses, and conversely that firefly flashes that occurred more than 3 s after exogenous input were spontaneous (endogenous). This conclusion is supported by both field and laboratory observations. Of 378 display-flashing periods recorded in 18 series, each from a different male of *Photinus pyralis* flying free in the field at 23° (ave. 6.15 s), only one was shorter than 4 s.[2] Similar results were obtained by Edmunds (1963) and Maurer (1968).

Though spontaneous STR and CIR flashing tended to be less regular than in the field, due to frequent flash-skipping, series of consecutive flashes were well within the reported range of field rhythm variability[2] (legends of Figs. 3, 5, and 7). The special case of 2–3-s pairs of apparently spontaneous flashes (Fig. 21; unfilled column caps in Fig. 19), is discussed below.

The SD ("reflex"?) response

Aside from irregularities in recorded flash form due to the motion of the CIR males, the SD photic responses observed in STR and CIR males differ in no essential respect from each other, or from those seen normally in free-flying animals.[3]

Short-delay photic interactions between males of *P. pyralis* had been observed in synchronized flashing among males courting the same female (Buck, 1935; Maurer, 1968) and between males flying indoors in darkness (Buck, 1938b), but it was not until the response was measured and studied intensively that it was recognized as part of the male's normal repertory (Buck *et al.*, unpub.). By programmed stimulation, the triggering was confined to the latter half of the flashing cycle (*i.e.*, more than 3 s after a male's flash)—an interval dubbed the "late window" to distinguish it from the 1.5–2.5-s post-flash "early window," which is tuned to the female's response and mediates orientation (Case, 1984; Buck, 1988).

In the field, the SD interaction occurs as a triggering of one flying male by the flash of a *close* neighbor or of an artificial light. The present laboratory-triggered delays are consistent with those measured in video records from free flying males (Buck *et al.*, unpub.). When male A thus triggers the flash of B, neither animal pays any attention to the other, but B's flashing rhythm is reset so that thereafter he flashes in synchrony with A (Case, 1984; Buck,

[2] The many hundred raw measurements in Buck (1936) that were given antique statistical treatment by Buck (1937) were reexamined to assess the range of individual period variation in free-flying males in nature. Using 38 series of 8 to 71 consecutive flashes, it was found: that a typical V value is 10, with values as low as 3 and as high as 20 occurring occasionally; that mean period decreases about 0.4 s for each degree (C) rise in temperature; and that statistically significantly different individual means occasionally occur even between two individuals at the same temperature. Nonetheless, as shown by Buck and Buck (1968, footnotes 42–47), the *P. pyralis* rhythm, though inferior in regularity to those of some tropical synchronizing species, is quite in line with many other biological periodicities, including human heartbeat during sleep.

[3] The variations were not necessarily due to the experimental conditions. Even in free field flashing, the magnitudes of all flash parameters show centrally peaked frequency distributions, and all vary with temperature. In considering photic effects on flash *timing*, flash initiation (with which this study is principally concerned) must be distinguished from flash *modulation*. Initial excitation depends on neuronal volleys from the brain (Case and Buck, 1963; Buonamici and Magni, 1967; Brunelli *et al.*, 1977) but there is some evidence that flash form (intensity, duration, time-course) may be affected also by activity of the final cord ganglia (Christensen and Carlson, 1981). The number, firing sequence, and areal distribution of the individual flashing units may also vary (Buck, 1955, 1966; Hanson *et al.*, 1969). Thus there are many potential sources of variation. Some STR records show flash form varying independently of the spontaneous flashing rhythm (Fig. 5), and between individuals given comparable stimulus flashes (Figs. 9–12). Aside from effects of changing firefly-photometer geometry, the same conclusions hold for the flashes of CIR males (Figs. 7, 8, 15–18, 20–24). The important point is that both the SD and LD photic responses maintain their characteristic and exclusive *delay* ranges independently of variations in flash *form* between individuals and between runs.

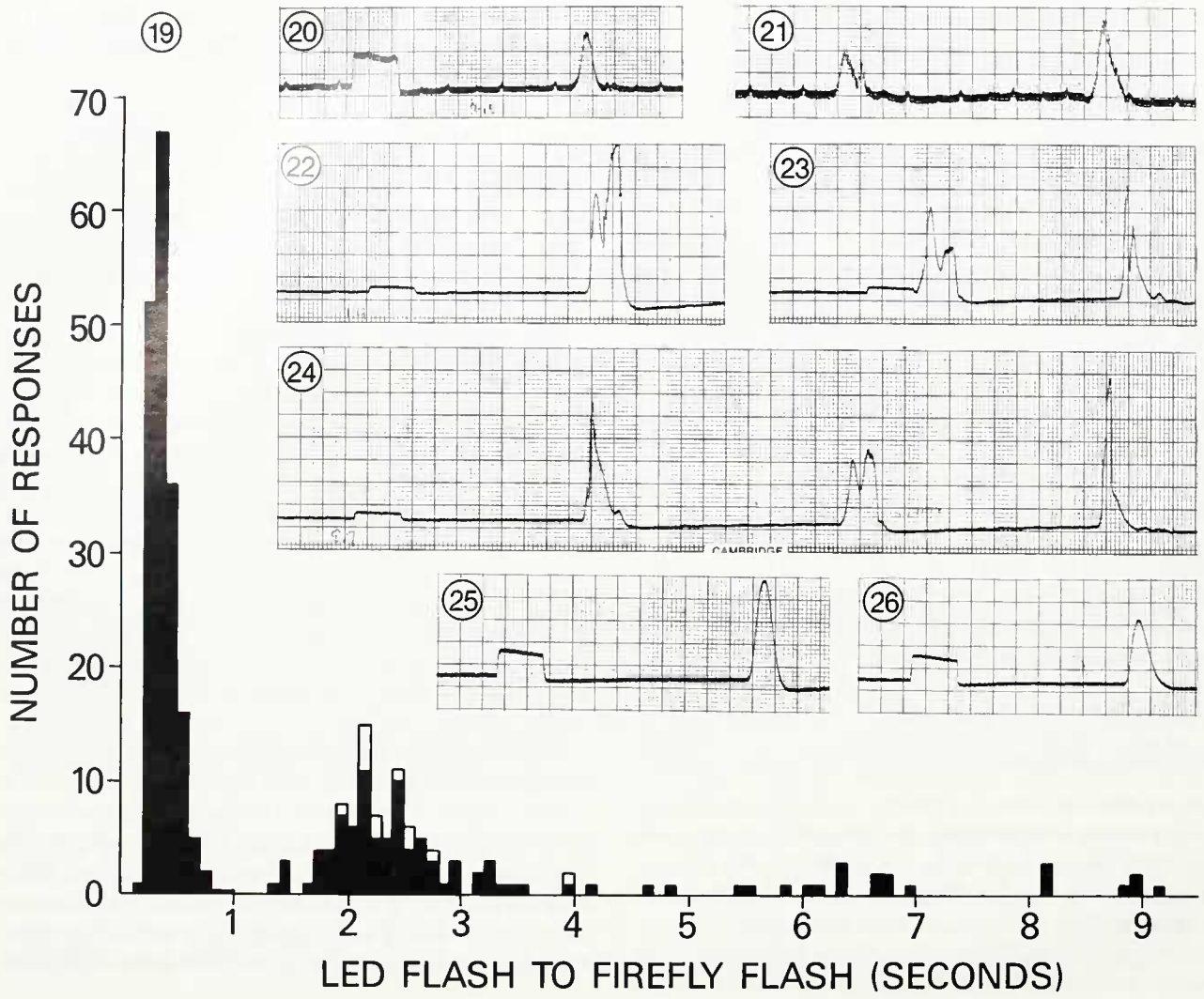

Figure 19. Frequency distributions of SD and LD responses. First peak (0.2–0.8 s) is the average of 180 SL responses of 6 STR males and 180 SD response of 6 CIR males (30 consecutive responses for each individual). Second peak (1.3–3 s) is 72 LD responses of the 10 CIR males that emitted more than one LD flash (filled columns), plus 11 corresponding spontaneous flash-to-flash intervals from the same males (unfilled caps). **Figure 20.** LD response of CIR male 107. Delay 1.96 s. **Figure 21.** Pair of spontaneous flashes 2.2 s apart. First flash was 11 s after previous flash. CIR male 107. **Figure 22.** LD response of CIR male 250. Delay 1.94 s. T = 22°. **Figure 23.** Rare apparent SD and LD responses to same LED flash. SD delay 0.44 s; LD delay 2.2 s. CIR male 250. **Figure 24.** LD response (delay 2.0 s), followed by two spontaneous flashes, the first 2.3 s later, the second 2.3 s after the preceding. CIR male 250. **Figure 25.** Normal response of freely perched female to LED flash. Delay 2.3 s. Female 1. **Figure 26.** Same as Figure 25. Delay 1.92 s. Female 2.

1988). The figures in the present paper are intended only to illustrate the variation range of the response. Its detailed aspects will be taken up in another paper. Its putative functions are discussed by Buck (1988).

The SD male-male triggering behavior in *P. pyralis* is also of interest because its delay is often not greatly different from that for flashes elicited by electrical stimulation in the head (Case and Buck, 1963). Similarly, the 0.3-s delay of the *L. lusitanica* male-male response (Papi, 1969) corresponds to the electrical brain delay in that species (Brunelli *et al.*, 1977). A 0.3-s photic response, distinct from the 0.6 male-female interval, has been found also in *P. concisus* and shown to correspond to the head-lantern electrical delay in that species (Hanson and Buck, unpub.). [It may also be the inter-male interval involved in the synchronized field flashing observed by Otte and Smiley (1977).]

Papi used the term "reflex" for the SD male-male in-

teraction interval in *L. lusitanica*, perhaps implying that it involves the sort of minimum brain-lantern delay expected in a nonspecific reflex—that is, a fixed response inherent in the way the flash-control system is constructed rather than one evolved specifically in a communicative context. (The human knee-jerk, a response incidental to the presence of stretch-receptors that function normally in locomotion, is a case in point.) In this vein, and because of the lack of interaction between free *P. pyralis* males after such triggering, I use "reflex" provisionally to suggest a possible qualitative distinction between the 0.38-s SD and 2.3-s LD photic responses.

The LD response (female-type circuit in male)

Because males of *L. lusitanica*, *P. concisus*, and *P. pyralis* respond (by orienting) to the characteristically delayed response flashes of their conspecific females, each must have a response-timing circuit that corresponds to the emission-timing circuit of the female. Males of *L. lusitanica* and *P. concisus* also flash in response to other, conspecific males, and after the same delay used by their respective females. This suggests that the timing process initiated by seeing a flash of light may, potentially, terminate by mediating either orientation or flashing. Whether this lability involves bifunctional or parallel circuits, and what determines whether female simulation occurs normally (*L. lusitanica*, *P. concisus*) or not (*P. pyralis*), are less important in the present context than the apparent presence in both sexes of the same emission-timing.

The 2.3-s (LD) signal-male delay induced in CIR *P. pyralis* males (23°) should presumably be shortened about 8% as a rotational correction, but is, in any case, close to the average 2.1-s response delay of *P. pyralis* females answering flashlight flashes at about 23° (Buck, 1937) or LED signals (Figs. 25 and 26). Thus, this laboratory finding appears to parallel Papi's SD finding and to strengthen the idea that emission-timing circuitry of the female type is also present in the male.

Why female-simulating behavior is overt in *L. lusitanica* and *P. concisus* and latent in *P. pyralis* is unknown. *P. pyralis* is the most abundant and widespread American photinid firefly, occurring in at least 23 states (Lloyd, 1966), whereas its sibling species, *P. concisus*, is limited to a small area of central Texas. These distributions are consistent with the expectation that a signal that identifies the female unambiguously would have selective advantage over one that does not. Possibly *P. pyralis* has evolved a step beyond *P. concisus*.

There were not enough spontaneous intervals of 2–3 s duration (Figs. 21, 24; unfilled column caps in Fig. 19) to assert that they derive from endogenous excitation of the same LD flash-timing circuit that is sometimes excited by LED flashes (Figs. 20, 22, 24). However, the concentration of such intervals strongly suggests that the stress of flying on the CIR suspension does induce spontaneous flashing at 2–3-s intervals in addition to the also atypical 2.3-s LD photic response to LED stimulation.

Use of male circuitry by female

In the three fireflies discussed above, the male recognizes the female's emission pattern specifically, but there is no evidence that the female recognizes the rhythmic spontaneous interflash interval of the male. However, in certain species in which the male's emission signal is a pair of flashes rather than a single flash, the female does recognize the male specifically. She responds only after being presented with a pair of flashes timed in the characteristic pattern of her conspecific male, and thus must have a circuit tuned to that interval. In *P. greeni*, for example, the male emits a pair of flashes 1.5 s apart every 5 or 6 s, and the female responds about 0.8 s after the *second* flash of the 1.5-s pair (Lloyd, 1969; Buck and Buck, 1972).

No instance has been reported of a female of a pair-flashing species mimicking her male's flash pattern in the field, but *P. greeni* females have been induced to flash in pairs 1.5 s apart by strong repetitive photic stimulation (Buck and Case, 1986). Thus, as with *P. pyralis* males forced to fly in tight circles, it appears that abnormal stimulation sometimes uncovers latent flash-timing capacity.

Significance and genesis of unisex flash-controls

In a cricket in which females cannot call, Huber (1962) found that females nevertheless ". . . possessed a nervous organization sufficient for primitive stridulatory movements in spite of the absence of stridulatory structures." Alexander (1962) suggested that if both sexes were at least potentially able to call ". . . it would represent an interesting simplification of evolutionary change in a communicative system—something of an assurance that the . . . song of the male and the ability of the female to respond to it . . . will evolve as a unit." The present evidence that male and female dialog fireflies share specific, quantitatively matched, flash-timing controls, overt or latent, may implement Alexander's insight.

Because males and females of dialog fireflies are almost identical in lantern structure and control mechanisms (Buck, 1948), the shortest photic delay circuit, if it is indeed a reflex, would be expected to be present in both sexes. It would be understandable, then, that this circuit could have been co-opted during evolution to mediate both the female's response delay and the matching recognition interval in the male (*L. lusitanica* and *P. concisus*), and to confer supplementary reproductive advantage via

male flash synchronization (Buck, 1988) in *P. pyralis* and *P. concisus*.

It is less obvious how and why, in some species, this potentially unerring clue to female identification has evolved (or retained) the ambiguity of being used by males as well as females. The surmise that dialog questions and answers ought to evolve as a unit seems not readily compatible with paradoxical behaviors like those in *L. lusitanica* and *P. concisus* in which males normally decoy other males as well as seek females. The existence of female-signal simulation seems to argue that the duplicate timing circuits owe their evolutionary fixation to that behavior, but it also seems obvious that dialog in which males can identify females unequivocally (as in *P. pyralis*) should be more strongly selected than dialog in which males are also attracted by males.

Among suggested functions of female-simulation, "improving the female's chances of fertilization" (Papi, 1969) implies altruistic group selection. "Giving a rejected male an opportunity to see and approach the female's flashed answers to another male, and thus another chance to mate with her . . ." (Lloyd, 1979) seemingly has the rejectee and the female synchronizing with each other as both flash in response to the primary male. This would require the rejectee to recognize a flash that not only did not occur at the proper female-recognition interval after his flash but was in a phase relation (simultaneity) that has been found, in other species, to be the point of minimum sensitivity to photic input (Buck *et al.*, 1981; Buck, 1988). It is also not at all clear that males giving the female-simulating response have, in fact, been rejected previously.

A third possible function of female-signal simulation—distracting the deceived male from courting the real female, and so boosting the decoy's statistical chances of finding a mate (E. Arbas and S. Lewis, pers. comm.)—may have more promise, particularly, as Dr. Lewis has pointed out to me, with the strongly male-biased operational sex ratio that is usual in dialog populations early in the season.

Summary

1. In timing her flashed answer to the male's signal, a female dialog firefly uses the same delay interval that the male uses in timing the interval between his own flash and her answer.

2. In three species, males answer the flashes of other males after the same specific response-delay interval that is characteristic of their conspecific females.

3. Experimentally, the male of a fourth species has been shown to be capable of flashing responsively after the same delay interval as the female. In a fifth species, the female can be induced to emit flashes with the same timing as one element of the male's spontaneous display.

4. The above data are compatible with the hypotheses that male and female firefly share some of the same courtship flash-timing circuits in overt or latent forms, and that a particular control circuit may, on occasion, time either detection or emission. The overall neurophysiological picture is of a pool of timing circuits that can connect in various input/output combinations to mediate a variety of behavioral patterns.

The data are consistent with Alexander's (1962) surmise that courtship questions and answers should evolve together. All present-day circuitry must, of course, derive by selection from ancestral flash-controls. In another communication I plan to compare firefly unisex responses with possible analogs in other animals, and to examine the speculation that duplicate circuits in conspecific male and female fireflies hark back to a stage in dialog evolution in which both sexes flashed alike.

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Literature Cited

Alexander, R. D. 1962. Evolutionary changes in cricket acoustical communication. *Evolution* **16:** 443–467.

Brunelli, M., F. Magni, and M. Pellegrino. 1977. Excitatory and inhibitory events elicited by brief photic stimuli on flashing of the firefly *Luciola lusitanica* (Charp.). *J. Comp. Physiol. (A)* **119:** 15–35.

Buck, J. B. 1935. Synchronous flashing of fireflies experimentally induced. *Science* **81:** 339–340.

Buck, J. B. 1936. Studies on the firefly. Ph.D. thesis, The Johns Hopkins University, Baltimore.

Buck, J. B. 1937. Studies on the firefly. II. The signal system and color vision in *Photinus pyralis*. *Physiol. Zool.* **10:** 412–419.

Buck, J. B. 1938a. A device for orienting and embedding minute objects. *Stain Technol.* **13:** 65–68.

Buck, J. B. 1938b. Synchronous rhythmic flashing of fireflies. *Q. Rev. Biol.* **13:** 301–314.

Buck, J. B. 1948. The anatomy and physiology of the light organ in fireflies. *Ann. N. Y. Acad. Sci.* **49:** 397–482.

Buck, J. 1955. Some reflections on the control of bioluminescence. Pp. 323–333 in *The Luminescence of Biological Systems*, Frank H. Johnson, ed. AAAS, Washington, DC.

Buck, J. 1966. Unit activity in the firefly lantern. Pp. 459–474 in *Bio-*

luminescence in Progress, F. H. Johnson and Y. Haneda, eds. Princeton University Press, Princeton, NJ.

Buck, J. 1988. Synchronous rhythmic flashing of fireflies. II. *Q. Rev. Biol.* **63:** 265–289.

Buck, J., and E. Buck. 1968. Mechanism of synchronous flashing of fireflies. *Science* **159:** 1319–1327.

Buck, J., and E. Buck. 1972. Photic signaling in the firefly *Photinus greeni. Biol. Bull.* **142:** 195–205.

Buck, J., E. Buck, J. F. Case, and F. E. Hanson. 1981. Control of flashing in fireflies. V. Pacemaker synchronization in *Pteroptyx cribellata. J. Comp. Physiol (A)* **144:** 287–298.

Buck, J., and J. F. Case. 1986. Flash control and female dialog repertory in the firefly *Photinus greeni. Biol. Bull.* **170:** 176–197.

Buonamici, M., and F. Magni. 1967. Nervous control of flashing in the firefly *Luciola italica L. Arch. Ital. Biol.* **105:** 323–338.

Case, J. F. 1984. Vision in the mating behavior of fireflies. Pp. 195–222 in *Insect Communication,* Trevor Lewis, ed. Royal Entomological Society of London. Academic Press, London.

Case, J. F., and J. Buck. 1963. Control of flashing in fireflies. II. Role of central nervous system. *Biol. Bull.* **125:** 234–250.

Christensen, T. A., and A. D. Carlson. 1981. Symmetrically organized dorsal unpaired median (DUM) neurones and flash control in the male firefly, *Photuris versicolor. J. Exp. Biol.* **93:** 133–147.

Edmunds, L. N., Jr. 1963. The relation between temperature and flashing intervals in adult male fireflies, *Photinus pyralis. Ann. Ent. Soc. Am.* **56:** 716–718.

Hanson, F. E., J. Miller, and G. T. Reynolds. 1969. Subunit coordination in the firefly light organ. *Biol. Bull.* **137:** 447–464.

Huber, F. 1962. Central nervous system control of sound production in crickets and some speculations on its evolution. *Evolution* **16:** 429–442.

Lloyd, J. E. 1966. Studies on the flash communication system in *Photinus* fireflies. *Misc. Publ. Mus. Zool. Univ. Michigan.* No. **130,** pp. 1–95.

Lloyd, J. E. 1968. A new *Photinus* firefly, with notes on mating behavior and a possible case of character displacement. *Coleopterists' Bull.* **22:** 1–10.

Lloyd, J. E. 1969. Flashes, behavior and additional species of nearctic *Photinus* fireflies (Coleoptera: Lampyridae). *Coleopterists' Bull.* **23:** 29–40.

Lloyd, J. E. 1979. Sexual selection in luminescent beetles. Pp. 239–342 in *Sexual Selection and Reproductive Competition in Insects,* M. S. Blum and N. A. Blum, eds. Academic Press, New York.

Maurer, U. M. 1968. Some parameters of photic signalling important to sexual and species recognition in the firefly *Photinus pyralis.* M. S. Thesis, State University of New York Stony Brook, NY.

Otte, D., and J. Smiley. 1977. Synchrony in Texas fireflies with a consideration of male interaction models. *Biol. Behav.* **2:** 143–158.

Papi, F. 1969. Light emission, sex attraction and male flash dialogue in a firefly, *Luciola lusitanica* (Charp.). *Monitore Zool. Ital.* (N. S.) **3:** 135–184.

Wallenstein, S. 1980. A test for detection of clustering over time. *Am. J. Epidemiol.* **111:** 367–372.